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Relationships Between Respiration, Weight Loss, Temperature and Moisture in Organic Residues on Tundra

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INTRODUCTION

Decay of biological materials progresses through the dissassociation of organically complexed molecules and elements with concomitant release of energy, molecules and minerals. A general hypothesis was previously reached by the International Tundra Decomposition Working Group that the main factors influencing decay rates in tundra ecosystems were temperature, moisture and substrate quality, in concert with other edaphic factors. Gilson, Dixon and other base adsorption respirometry measurements have been used as indices of microbial activity in soil, humus, litter and standing dead leaves. These methods were used also to monitor the effects of temperature and moisture on microorganism metabolism within organic remains. Independent weight loss determinations have been made at almost all of the IBP tundra sites (Heal & French, this volume).

This paper compares the measurements of weight loss and respiration in experiments performed at the respective national sites and reports the effects of moisture, temperature and age of substrate on respiration and decomposition rates in the sites.

MATERIALS AND METHODS

Barrow, Alaska, USA

Plant samples collected in the field at Barrow in the summer and fall of 1970-73 were returned to laboratories in Barrow and Fairbanks, air-dried, sorted and analysed for major constituents (Jermyn, 1955). Individual plant leaves studied were of *Eriophorum angustifolium* and *Carex aquatilis* collected from virtually pure stands of the species in the Site 2 study area. Mixed litter from a number of species was also collected from the soil surface at Sites 2 and 4. Site 2 has a wet meadow vegetation dominated by carices, mosses and graminoids. Site 4 is a low centered polygon system dominated by carices but with sparser vegetation on the basin and ridges than in the troughs.

Entire plants including standing dead leaves were harvested each time. Standing dead was separated from green material and further separated chronologically into leaves aged 1, 2 and 3 years. These aged leaves as well as green midsummer growth, August growth, and moribund September leaves were placed in Gilson differential respirometer flasks to assess the rate of decomposition through measurement of O_2 uptake. A minimum of three but in most cases 6-10 replicate results were obtained to determine the mean rate and standard error. The effects of varying temperature and moisture on respiration were intensively measured over the range of-7.5° to +10°C and 10% to 2000% H_2O dry weight. Experiments with temperatures up to 40°C were performed in the 100% — 600% moisture range.

Oxygen uptake was translated into CO_2 loss after base titration experiments had determined the most common R.Q. in litter to be 1:0.85 (O_2:CO_2). Weight loss in respiration, calculated directly from CO_2 loss, was compared with weight loss measured in litter bags in the field. Litter contained 50% carbon, and total percent weight loss was calculated as carbon loss × 100/% carbon. The weight loss in respiration was calculated using bihourly field temperature measurements and summed over 100 days. Moisture levels in the experiments were set equal to those measured in the field on appropriate days. Soil respiration data available in the literature (Douglas & Tedrow, 1959) were used to estimate approximate rates of weight loss from Barrow soils in the same manner as outlined above. The total weight loss at the end of the period was added to the weight loss figure attributable to substrate dissolution concomitant with carbon loss.

Hardangervidda, Norway

The Hardangervidda study area in south Norway included five decomposition study sites, varying in vegetation and substrate as described in Norwegian IBP reports. There were three sites at Stigstuv:

Dry Meadow: mostly litter of *Dryas* and *Salix* leaves and shoots mixed with various mosses, graminoids and carices.

Wet Meadow: plant residues of mainly *Carex nigra, Salix* spp., *Drepanocladus* and *Philonotis fontana.*

Lichen Heath: mixed lichen cover and intermittent growth of *Empetrum* sp., *Vaccinium vitis ideae,* and *Carex bigelowii.*

Two further sites, a snowbed at Finse and a birch wood at Maurset, were studied. The general aims were: 1) to obtain representative mean values for soil respiration in the field during the growing season, 2) to define temperature and moisture relationship with soil respiration, and 3) to compare measured and calculated respiration rates with decay rates found by use of the litter bag technique.

The soil respiration experiments were carried out between early July and September 1972.

The apparatus for measuring respiration (Fig. 1) consisted of an iron ring, 20 cm in diameter and 8 cm high, which was inserted into the soil after the vegetation had been clipped. The rise in respiration due to disturbance was found to decline after the first 15-20 minutes.

A plastic cuvette was connected to the iron ring against a rubber gasket and fastened. Inside the cuvette a fan mixed the air during the experiment. A plastic bag connected to the open air compensated decreasing air pressure inside the quvette during sampling.

A Dräger Multi Gas Detector connected to a test tube containing hydrazine chromagen produced a colour reaction relative to the CO_2 content of the air. Results were obtained in % CO_2. The open air CO_2 content found by several experiments was subtracted.

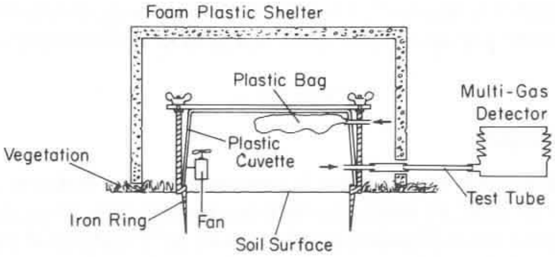

Fig. 1. Apparatus used for measuring soil respiration in the Norwegian studies.

Experimental time was chosen dependent on climatic conditions and expected site variations, to give a respiration rate in the range where the test tube had the best scale for the most accurate reading of the result. Assuming a linear increase in the CO_2 concentration with time during the experiment, half of the time needed to take out the air sample was included in the experimental time.

During each experiment the soil surface temperature was measured both inside (ITEMP) and outside the cuvette. A foam-plastic shelter was used to avoid a greenhouse effect inside the cuvette. Despite this precaution the internal temperatures were about 1.0°C higher than the external, and the respiration rates are calculated with reference to internal temperatures.

After each experiment a sample of litter and soil was taken from the top 2 cm for determination of soil moisture content. For about half of the experiments carried out, the air moisture content inside the cuvette was determined in mg/l, by use of an aqueous vapor test tube. Relative air moisture in %, 10 cm above the soil surface, was observed for each experiment at the climatic station close to the experimental plots.

The results are expressed in mg CO_2/m^2 hr, by the equation:

$$\text{mg } CO_2/m^2 \text{ hr} = \frac{V_c \times C_{co_2} \times 60 \times Spw_{co_2}}{100 \times A_c \times E_{time}}$$

V_c = Volume of the cuvette in ml.

C_{co_2} = Measured concentration of CO_2 in % ÷ open air CO_2 concentration

Spw_{co_2} = Weight of CO_2 in mg/l at the experimental temperature

A_c = Base area of the cuvette in m^2

E_{time} = Experimental time in minutes

At sites with permeable soil and especially under dry weather conditions, the respiration results include below soil surface respiration. This is shown experimentally by decreased effect from the air pressure-compensating plastic bag which is estimated to compensate for about ⅔ of the volume of air sample removed. These respiration results measure the total soil respiration, including respiration from plant roots, rhizomes and soil invertebrates.

To get results comparable with measurements from other IBP tundra sites, and to calculate weight loss through carbon loss due to respiration, data in mg CO_2/m^2 hr were recalculated as μg C/g dry weight of organic matter in the top 2 cm/hr (or 24 hr).

The *in situ* measurements of soil respiration also include some CO_2 released from below the soil surface. From the plastic bag correction it seems realistic to calculate the measured CO_2 output as output from the top 2 cm of the soil, including litter layer when present.

The recalculation is done using mean values for soil bulk density at each site. The organic matter content of soil is expressed by use of mean values determined in approximately 100 samples from each site. Bulk density was estimated in relation to grams of organic matter per gram soil after ignition of soil samples (Jeffrey, 1970).

Other Sites

United Kingdom and Ireland

At Moor House in Britain the approach concentrated on nutrient and weight loss and nutrient studies as well as respirometric measurements. Respiration of organic materials was measured with Dixon manometers at 10°C and field moisture between 20% and 600% (dry weight). Measurements were made on leaves of *Eriophorum* and *Rubus* and on shoots and stems of *Calluna*. Site and soil descriptions for Moor House may be found in Latter *et al.* (1967) and Heal & Smith (in press).

In the Irish study leaf material of *Festuca* and *Molinia* was studied in a Gilson respirometer at 18.5°C and 27°C through a moisture range from 20%-800% dry weight.

Signy Island, Antarctica

Data are from a *Chorisodontium* moss bank. Respiration was measured in a Dixon manometer (Baker, 1970).

Fairbanks, Alaska, USA

L, H, and F layers in a typical taiga birch forest near Fairbanks were studied intensively in Gilson respirometers. Temperature and moisture ranges were -5°C to +40°C and 10% to 700% respectively. These data were generously given by Dr. Keith Van Cleve.

RESULTS AND CONCLUSIONS

Barrow, Alaska, USA

Effects of temperature on carbon loss in respiration

Fig. 2a shows the effect of temperature on carbon loss from total litter and one-year-old leaves of *Carex aquatilis* from Barrow. Respiration occurs at −7.5°C and the rate increases rapidly with increasing temperatures. Q_{10} values range from 6 in the −7°C to +3°C range to 3.8 in the 15 to 25°C range. Values lie between 4 and 3 in the ranges between 0°-10°C and 20°-30°C. Temperature effects on decompositon at Barrow are very closely interrelated with moisture levels, substrate age and microbial biomass.

Effects of moisture on carbon loss in respiration

In Barrow the microorganisms in plant remains do not respire at moisture levels below 20% dry weight (Fig. 2b). At any given field temperature in the range generally encountered during summer months at Barrow the effect of increasing moisture above 25% is to increase respiration rate. In general moisture levels in excess of 300% depress microorganism respiration rates. However, the moisture regime which begins to attenuate respiration rate differs for varying temperatures (Fig. 2b and 4). From these figures it can be seen that at Site 2 at higher temperatures, increasing moisture reduces microbial respiration within litter. At lower temperatures high moisture levels do not exert their depressing effects so sharply and maximal respiration continues throughout a much wider range of increasing moisture levels.

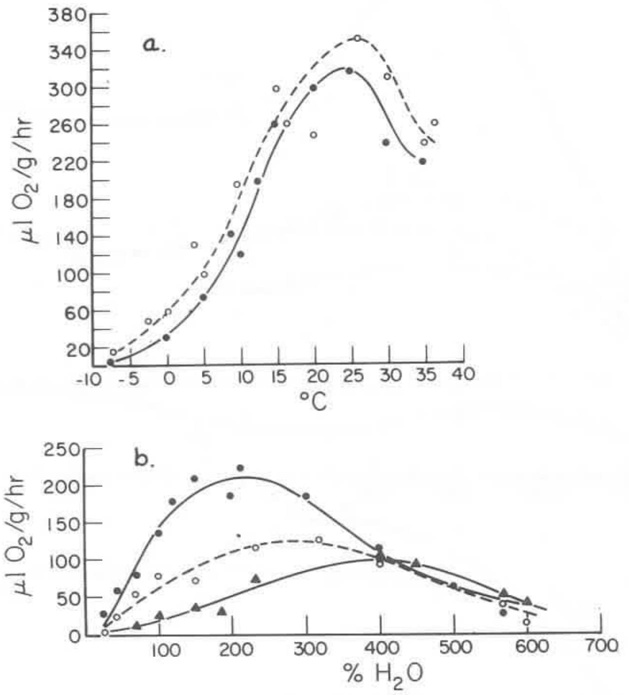

Fig. 2. Respiration response, Barrow, Alaska, USA. Curves are eye-plotted. a. Respiration response to temperature at 120% moisture. Points are the means of 6 samples, 10 readings per sample. Deviation from the mean ranged between 8 and 25% from the low to the high temperature respectively. ○ *Carex aquatilis.* ● *total litter, Site 2. b. Respiration response in litter to moisture at different temperatures. Points are the means of 10 samples, 10 readings per sample. Deviation between 20 and 500%* H_2O *± 12% of mean, between 500 and 700%* H_2O *± 30% of mean.* ▲ *0°C,* ○ *5°C,* ● *10°C.*

At Site 2 these moisture/temperature relationships exist for all categories of plant remains tested, i.e. one-, two- and three-year-old standing dead of *Carex* and *Eriophorum* as well as for total litter on the ground surface. On Site 4 the response surfaces are obviously different from those on Site 2 (Fig. 3a). Two to three hundred percent moisture was optimal at all temperatures tested. Increasing moisture here does not have so sharp an effect and temperature does not shift the moisture optima so sharply.

Interacting temperature and moisture

Respiration experiments aimed at determining optimum moisture and temperature levels for decomposition at Barrow revealed that the optima were interdependent. The greatest extremes in response of decomposition rate to variation in moisture levels are exhibited at approximately the optimum temperature. Similarly, extreme response to variation in temperature is seen at approximately the optimum moisture level. The system showed a marked tendency for the optimum moisture content for respiration to be higher at lower temperatures and for the optimum temperature for respiration to be higher at lower moisture levels.

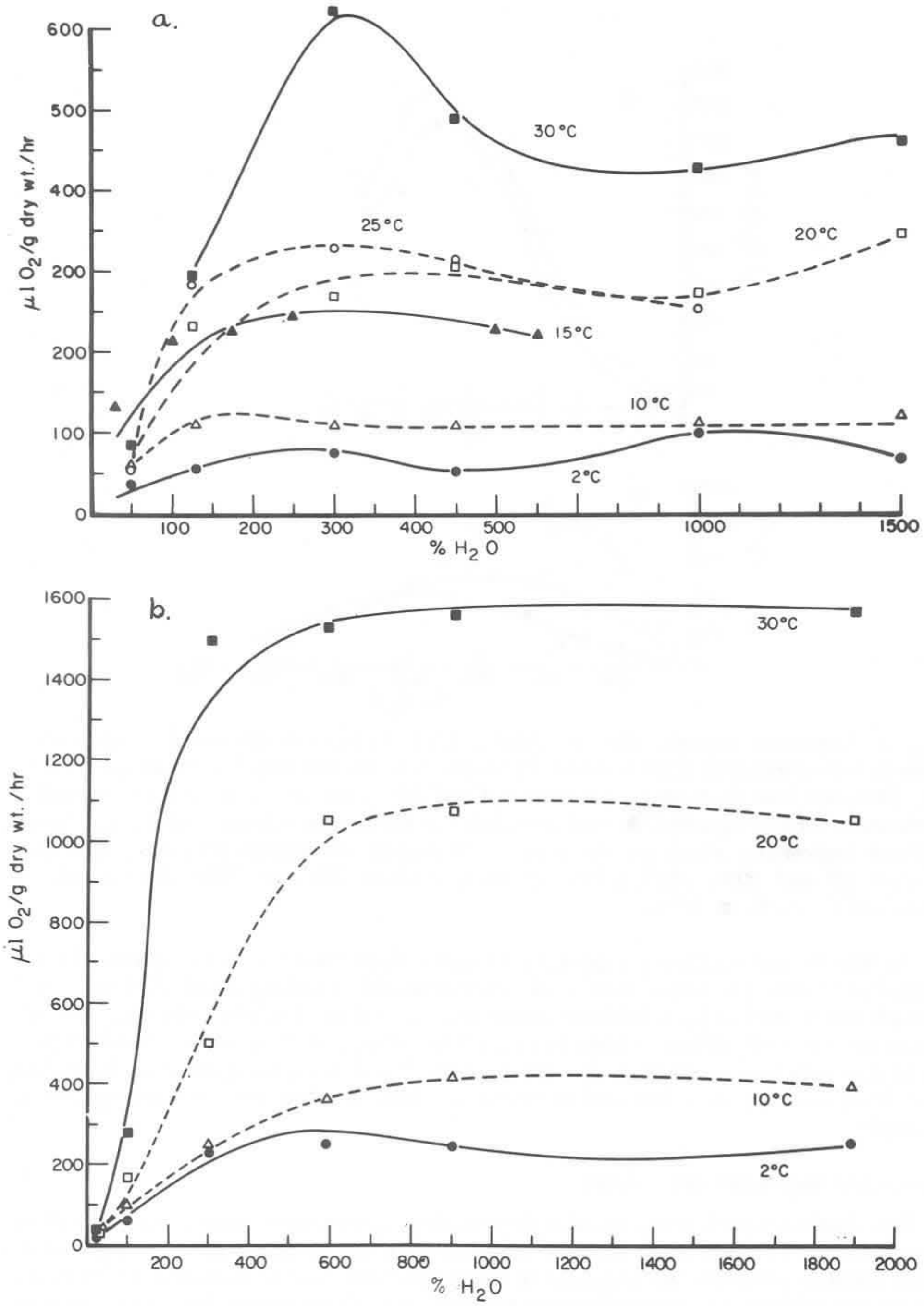

Fig. 3. a. Litter on Site 4 at Barrow. Points are the means of 3 samples, 6 readings per sample. Variation about means never more than ± 10%. Curves are eye-plotted. b. Oxygen enrichment of Barrow litter, the air being replaced by 100% oxygen. Points are the means of 3 samples, 6 readings per sample. Variation around points never more than ± 5%. Curves are eye-plotted.

These considerations made it impossible to determine the precise optimum conditions for decomposition at the Barrow site. Approximate optima for both parameters were recorded so that optimum moisture was in the range of 120-400% H_2O in the approximate optimal temperature range of 23°-28°C.

The effects of temperature were superimposed on the moisture effects. Three-dimensional respiration response surfaces through the range of moisture and temperature were constructed for litter and chronologically separated standing dead residues of *Eriophorum angustifolium* and *Carex aquatilis*. The surfaces in the figures were generated from three replicate readings for each set of intersecting parameters. For litter (Fig. 4) the surface was generated from 90% real data while the surfaces in Fig. 5 were constructed on a 75% data base. Where an actual data point was missing it was derived from an average of the four nearest points. These figures emphasise that respiration in microorganisms at Barrow is a function governed by several independent variables besides temperature and moisture. Third and fourth variables, substrate age and biomass of resident microorganisms also need to be estimated in order to gain a holistic view of the process and its functioning in decomposition.

Fig. 4 and 5 represent the Gilson measured respiration rates of Barrow litter and standing dead between −10° and +10°C and at moisture levels between 10 and 700%. Generally the respiration temperature relationship has a $Q_{10} = 4$. Moisture is optimal at approximately 300% for temperatures over 5°C and at 400-500% for temperatures between +5° and −5°C.

Fig. 4 and 5 show that the higher moisture contents have less effect in slowing respiration at lower temperature than at higher temperature. The slopes of the moisture curves (Fig. 5) generally decrease with decreasing temperature. The surfaces show some interesting features, especially in relation to the chemical analysis in Table 1 and the data in Fig. 2a and b. Fig. 5 also shows that as organic matter decomposes (excluding leaching) the respiration rate decreases, i.e. the decomposition rate decreases. In one-year-old material respiration is 1.2 times faster than in two-year-old material (Fig. 5c and f) and about 1.5 times faster than in 3-year-old remains. Data for the latter are incomplete and respiration surfaces have not been constructed. The figures show also that at low temperatures and low moistures standing dead remains maintain higher respiration rates than total litter. Present interpretation of this observation is that standing dead material is in a position in the canopy where temperatures and moistures are generally lower than at the surface litter layer and that consequently microorganisms in standing dead are more adapted to decomposition in these regimes of dryness and lower temperatures. Our analysis of fungal populations in litter and standing dead (Flanagan & Scarborough, this volume) tends to

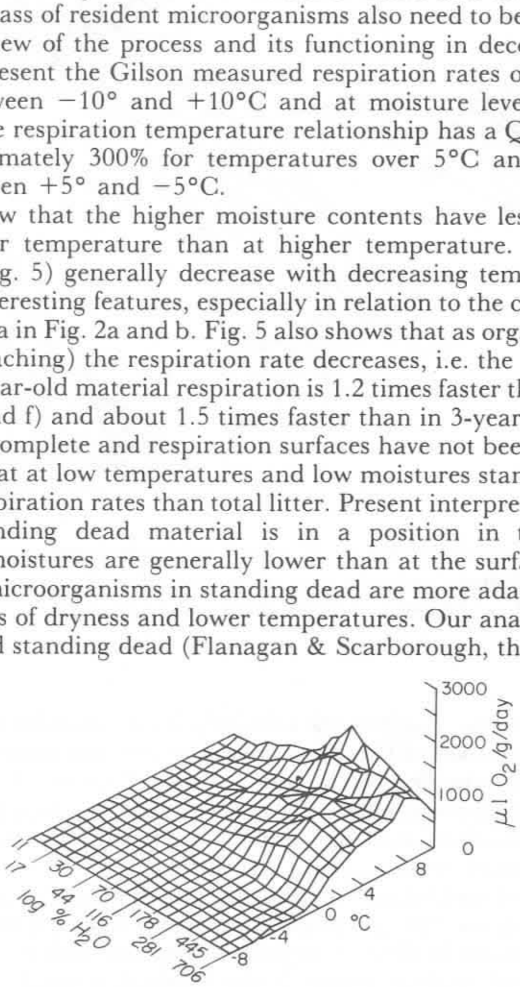

Fig. 4. Respiration of total litter in relation to temperature and moisture, from Barrow Site 2.

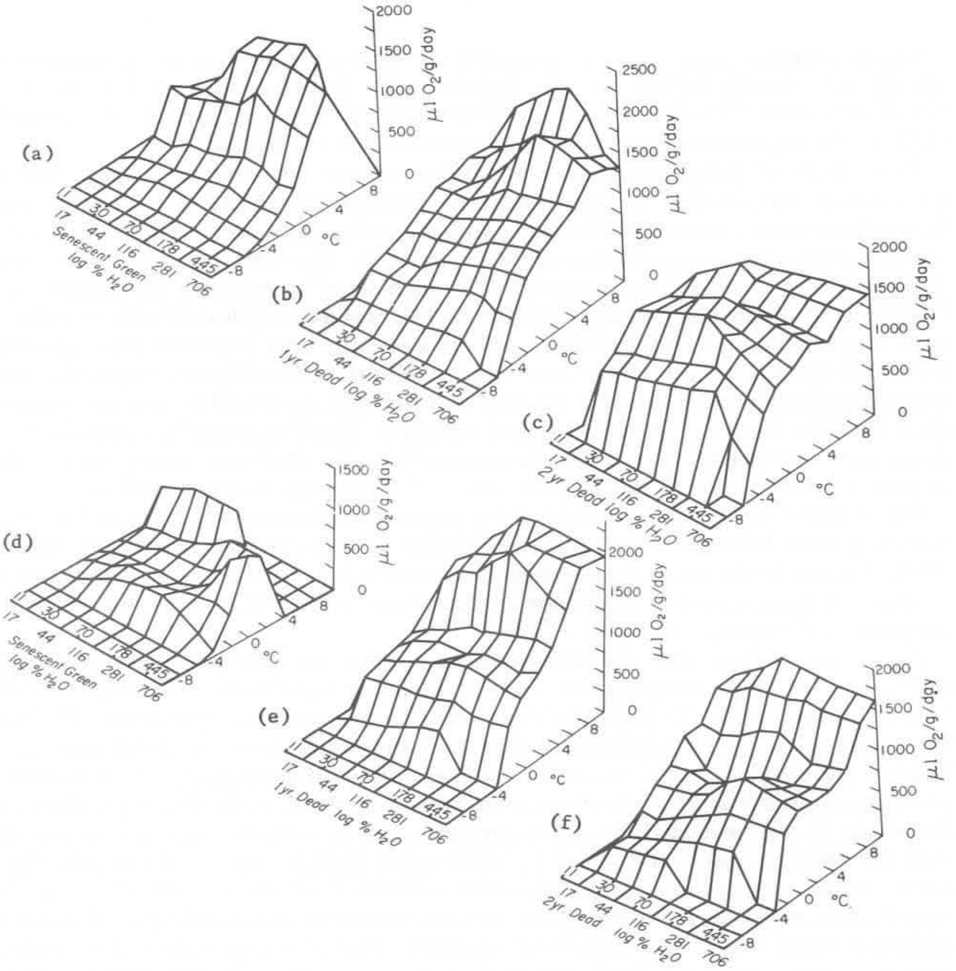

Fig. 5. Respiration of plant material in relation to temperature and moisture; a, b and c are Eriophorum angustifolium *senescent green, 1 year standing dead, and 2 year standing dead respectively; d, e and f are* Carex aquatilis *of the same categories.*

support this hypothesis. Further, the relatively intact vascular elements in standing dead may be holding most of the water present at very low moisture levels so that the moisture levels within the elements would be higher than overall figures indicate. This could account for high respiration rates at seemingly low moisture levels in standing dead. Higher respiration rates in standing dead are presumably due in part to remaining, more easily decomposable substrates.

The recently dead and/or senescent green/brown plant remains at Barrow, while rich in readily available carbon compounds, do not produce high respiration rates. The microbial biomass in these materials is very low and we believe that the low respiration measured in these tissues is due to small populations of decomposition organisms.

Oxygen and moisture interactions

Preliminary experiments with oxygen enrichment of Gilson flask atmosphere during litter decomposition have revealed (Fig. 3b) that with added oxygen the "hump" shape of the respiration-moisture curve disappears. Additionally, oxygen enrichment greatly increases the respiration rate. The latter most likely reflects a large increase in growth as well as respiration in the O_2-enriched environment. It emphasises that increasing moisture in organic remains (most probably) decreases decomposer respiration through displacement of air and reduction of oxygen diffusion since, when oxygen is added, respiration levels are maintained through increasing moisture levels. There is need for more precise study in this area.

CO_2 levels in the substrate microenvironment may also exert their influences on microorganism metabolism. Generally, increasing CO_2 levels decrease respiration. Replacement of increasing CO_2 concentrations with O_2 could help account for increased respiration rates.

Referring again to Fig. 5 it can be seen that while decomposition surface dimensions decrease with time the general responses in relation to temperature and moisture remain the same. These considerations have led the US group to use statistically validated points in the respiration response configurations of Fig. 5 as driving variables in simulation models of tundra decomposition. These models will, hopefully, be able to predict decomposition rates for US and other tundra sites.

Decomposition below ground at Barrow

The temperature/moisture organic matter relationships discussed above refer only to above-ground respiration rates but comparisons with published data from Barrow tundra sites reveal some moisture and temperature relationships with respiration for different levels in the soil organic matter profiles (Douglas & Tedrow, 1959).

In soils of the upland tundra type which dominate in parts of the Barrow area, Douglas & Tedrow (1959) showed that very low levels (<100%) of moisture decrease decomposition and respiration rates, especially at higher temperatures. The converse situation is also true for Barrow soils where at low temperatures little change in respiration occurs with increasing moisture content.

Because fluctuations in moisture content decrease with depth from the surface the significance of temperature in regulating decomposition rates must increase with depth. Conversely, because litter and standing dead moisture levels fluctuate widely within short time intervals it is likely that moisture in these areas is exerting a greater influence than it does at depth. The influences of moisture would therefore be greatest in litter and standing dead at spring break-up and before and after heavy rainfall. Also, because respiration within litter and standing dead must respond to wider extremes of temperature and moisture decomposition attains minimum and maximum values more frequently than in soils.

From the data presented by Douglas and Tedrow it can also be shown that when soil organic content increased, as in their half-bog site with organic content of 66.6%, moisture did not become limiting until the 500% level at 19.5°C. At the same temperatures moisture was limiting at the 70% and 30% levels in the peaty high-centre polygon and upland tundra soils with a 36.9% and 13.1% organic content respectively. No litter or standing dead remains ever have so low an organic content as the latter. Microorganism response to moisture in the half-bog soil with 66.6% organic matter most closely approximates the moisture response of litter and standing dead microorganisms whose substrate has an organic content of about 95% in our experiments. This interaction of moisture with organic content is presumably due to structural more than biological factors, e.g. an organic substance as compared with mineral soil will have lower bulk density, be more hygroscopic and have more aeration spaces allowing of higher oxygen content.

Comparison of respiration predicted weight loss and weight losses measured directly in the field at Barrow

Above ground. The weight loss due to exit of carbon in respiration from Barrow litter calculated as described on the second page of this paper is expressed in Fig. 6. Similar figures can be generated for one-year-old standing dead of *Carex* and *Eriophorum*. The moisture and temperature regimes are typical for Barrow during the field season. The temperature minima and maxima were derived from Weller & Benson (1971). Taking carbon as constituting 50% of the plant remains we predicted from respirometry measurements that from June to September 1971 the plant litter and standing dead decreased in weight by between 10.1 and 11.8%. Litter bag weight loss determinations for the same period show a total weight loss of 9.9% ± 1.8% (Fig. 6).

Below ground. Estimates of weight loss relative to loss in respiration were also made based on the moisture and temperature levels and influences presented by Douglas & Tedrow (1959). For Arctic brown soil to 1-inch depth we calculated that carbon loss from that soil organic profile was at the rate of 3.7% of organic matter for the field season of 1957. Weight loss at 0-4-inch depth was estimated at 0.75%. Respiration rates and carbon loss estimates for the upland tundra soils studied by Douglas & Tedrow were much higher for the same range of temperatures and moisture levels than in Arctic brown soils. Estimates from their figures and regression curves suggest that the organic matter in these soils was decomposing from 1.3 to 2.4 times faster than plant remains in the Arctic brown soils at 1-inch depth. This could mean that weight loss in the organic matter from 0-1-inch depth in upland tundra is at the rate of 4.8-8.8% per decomposition season at Barrow, i.e. at approximately two-thirds the rate of total litter decay in Barrow Site 2. However, these figures do not include a calculation of root respiration which could account for 30%-50% of respiration in soils (Monteith, Szeicz & Yabuki, 1964; Macfadyen, 1970).

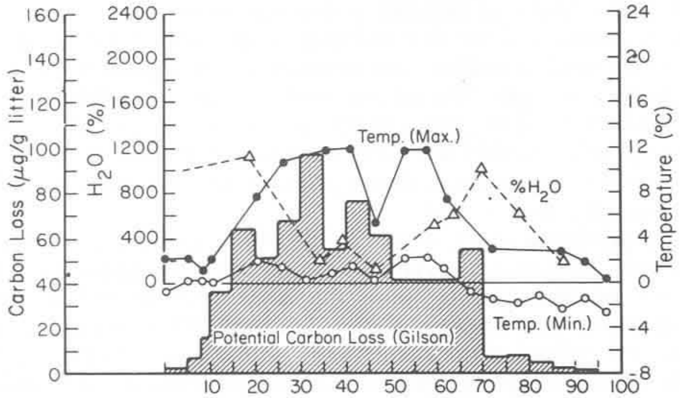

Fig. 6. Carbon loss from Barrow total litter calculated from respiration measurements corrected for field temperature.

From estimates of respiration rates and standing crops of soil organic matter, it was calculated that approximately 15 g/m^2 of standing dead, 26 g/m^2 of litter and 100 g/m^2 of soil organic matter are recycled each year totaling 141 g/m^2 in the top 1 inch. Beneath the litter zone in Barrow plots, the organic content is between 75% and 90% to a depth of 1 inch and the bulk density is from 0.1-0.3. Below this depth significant carbon loss occurs in respiration but data are not complete.

Other measurements of weight loss. The effects of moisture as running water, and temperature changes at freezing and thawing, influence weight losses drastically. The most noticeable changes in weight, chemical quality and quantity of plant remains occur from August of one year to June of the next. During this time dead plant leaves at Barrow lose up to 30% of their original weight as green live leaves. This loss may be due to downward translocation in attached leaves and/or a number of successive mechanical processes, associated with leaching, freezing, thawing, and further leaching. Portions of this loss may be attributed to microbial respiration and assimilation, particularly in the fall and early spring when temperatures are above −7.5°C and gaseous moisture is available. The translocation and/or leaching processes during and immediately after death can recycle approximately 60.0 g/m^2 year if primary production rates are around 200 g/m^2 year above ground. This amount of leaf material was produced in the *E. angustifolium* stand during the summer of 1972.

Microbial decomposition recycles 141.0 g/m^2 year of organic matter while downward translocation and/or leaching accounts for recycling of 60.2 g/m^2 year. Thus about 200 g/m^2 year may be recycled in a depth of 1 inch. This figure does not include the substrate utilisation in microbial tissue production and consequently does not reflect a true picture of substrate dissolution rates. If the efficiency of conversion of substrate to microorganism material, i.e. the yield coefficient, = 0.35 then the figure 141 g/m^2 year would have to be amended and a figure nearer 217 g/m^2 year may be a better reflection of dissolution rates. The yield coefficient of microorganisms using lignocellulose (Table 1) as main substrates may be much lower than 0.35. The latter figure is from Babiuk & Paul (1970) based on chemostat estimates. Waksman (1932) gives a yield coefficient for bacteria of 0.05-0.10 and for fungi 0.2-0.4, i.e. an average coefficient of 0.25. Based on this coefficient the amount of organic matter recycled annually is 188 g/m^2.

These results and calculations for Barrow indicate that respiration and weight losses for each type of organic matter examined are primarily correlated with microbial biomass, substrate quality and quantity, temperature and moisture. Temperatures in excess of 30°C decrease respiration drastically at any moisture content. Respiration measurements of O_2 consumption were made to −7.5°C consistently.

The ability of decomposer organisms to respire at −7.5°C may allow them to extend their active period beyond that of primary producers by as much as one month in the spring and by at least one month in the fall.

While temperatures rarely, if ever, attain optimum levels for decomposition in Barrow, moisture levels are frequently in the optimal range. Moisture affects decomposition most dramatically at approximately optimum temperatures. In Barrow, therefore, moisture may never exert its maximum influence because temperature never attains optimum. Considering the psychrotolerant nature of Barrow respiration processes it is reasonable to state that temperature is more important than moisture in determining seasonal rates of respiration in Barrow tundra. The importance of even short periods of high temperatures (> 12°C) to decomposition rates in Barrow is emphasised when a calculation for daily respiration is made based on daily mean rather than on bihourly temperatures. Carbon loss in the latter calculation is 1.5-2.5 times that in the former.

Table 1. Analysis of major constituents in Barrow plant residues.
Results are expressed as % dry weight.

	Green material	Senescent green	*1 yr standing dead*	*2 yr standing dead*	*3 yr standing dead*	*Total litter*
			Carex aquatilis			
EtOh soluble	26.6	21.0	11.7	4.7	6.6	5.4
Pectin/starch	8.4	6.1	8.8	10.2	6.9	7.5
Cellulose	32.5	40.3	43.8	49.3	44.0	38.7
Lignin	25.1	28.6	27.7	29.5	37.7	37.9
Ash	6.3	6.4	5.2	7.0	6.7	4.8
Volatiles	6.7	4.4	8.1	7.0	3.0	9.0
			Eriophorum angustifolium			
EtOh soluble	27.2	24.0	6.8	4.5	4.1	
Pectin/starch	7.5	5.0	7.6	7.3	9.6	
Cellulose	32.0	40.2	43.4	45.5	34.3	
Lignin	25.5	27.5	33.0	34.0	48.9	
Ash	4.6	4.5	4.4	4.0	7.2	
Volatiles	7.6	2.7	7.9	7.5	2.8	

The standard error of the mean of three replicates was never more than ±8% of the mean.

Regression analysis of litter respiration data with respect to moisture alone explains less than 20% of the variation although correlations are significant at the 1% level. Temperature alone explains 40% of the variation. With interactive terms for moisture including the negative quadratic term and the exponential ($Q_{10} = 4$) temperature relationship 63% of the variation is explained ($r = 0.797$, $p < 0.001$):

$$R = 3.4 + 0.29 \times (e^{0.1386t}) \times M - 0.004 \times (e^{0.1386t}) \times M^2$$

where R is respiration (μl O_2/g hr), t is temperature (°C), and M is moisture expressed as g/g dry weight.

Norway

Temperature and moisture relationships with soil respiration

In the analysis of soil respiration data from the Norwegian sites respiration rates, expressed as carbon loss from organic matter in the upper 2 cm of litter and soil, were regressed against temperature, moisture, and temperature plus moisture. Both linear and curvilinear expressions were used and the correlation coefficients are summarised in Table 2.

Temperature. In situ measurements of soil respiration were made at temperatures from 0.5°C to 21.0°C. No data are available on respiration at sub-zero temperatures.

Table 2. Correlation coefficients for Hardangervidda soil respiration.

Sites and horizons	*A-A*	*St-A*	*LH-A*	*DM-A*	*WM-A*	*BF-A*	*SB-L*	*SB-F+H*
No. of data	*267*	*154*	*48*	*49*	*57*	*58*	*11*	*44*
Respiration								
(μg C g^{-1} om day^{-1})								
T	.368*	.467*	.779*	.769*	.646*	.484*	.664	.759*
M	.450*	.498*	.066	.039	.234	.226	.401	.360
$M + M^2$	.570*	.630*	.276	.371	.289	.296	.407	.383
$M + M^2 + M^3$	.615*	.695*	.276	.407	.332	.297	.485	.383
T×M	.538*	.587*	.485*	.560*	.132	.062	.742*	.167
$T \times (M + M^2)$	.731*	.798*	.672*	.709*	.581*	.515*	.847*	.331
$T \times (M + M^2 + M^3)$	.783*	.870*	.795*	.785*	.794*	.549*	.884*	.588*
Log resp								
T	.408*	.465*	.813*	.788*	.531	.463*	.724	.724*
Q_{10}	4.2	5.2	3.6	3.1	3.0	1.9	4.9	3.0
Resp								
e^{qt}	.327*	.405*	.820*	.777*	.682*	.488*	.574	.773*
$e^{qt} \times M$	.573*	.629*	.720*	.733*	.213	.008	.813*	.068
$e^{qt} \times (M + M^2)$	.778*	.855*	.815*	.786*	.662*	.493*	.844*	.457*
$e^{qt} \times (M + M^2 + M^3)$	.800*	.873*	.860*	.818*	.819*	.560*	.875*	.697*
where $q = \frac{\ln(Q_{10})}{10}$								

* = significant at 1% level.

Sites

A = All
St = 3 Stigstuv combined
LH = Lichen heath
DM = Dry meadow
WM = Wet meadow
BF = Birch forest
SB = Snowbed

Horizons

A = All
L = Litter
F = Fermentation
H = Humus
T = Temperature
M = Moisture

In regression analysis of data exponential temperature relationships were generally better than linear for all sites separately and in combination. The dry sites gave generally better correlations with temperature (Table 2) than the wet sites, particularly with exponential relationships. The exponential temperature relationship has a Q_{10} in the region 3-5 over the range of sites. The higher values are seen in the drier sites, although the highest value is found in the combined Q_{10} relationship for the Stigstuv sites.

Moisture. Moisture relationships were examined by the addition of moisture terms to the regression multiplicatively with temperature including quadratic and cubic moisture terms, i.e. $t \times m$ and $t \times (m + m^2)$ and $t \times (m + m^2 + m^3)$. In all cases addition of nonlinear terms improved the correlations. However, the improvement was only large enough to represent "real" differences when the moisture range extended beyond the site optima. This is shown particularly in the differences between the L and F + H layers of the snowbed (Table 2).

Temperature and moisture combined. From the combined regressions outlined above it was possible to construct regression surfaces for the Hardangervidda sites (Fig. 7).

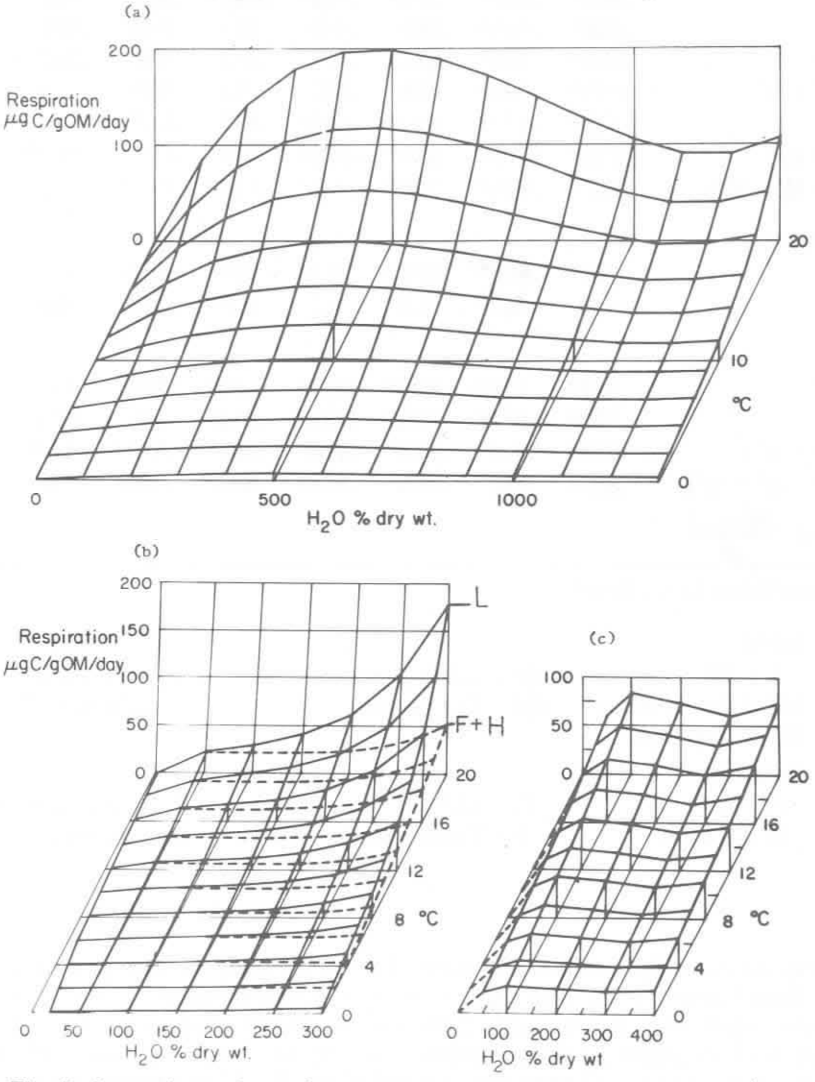

Fig. 7. Regression surfaces of respiration with temperature and moisture for a) 3 Stigstuv sites together, b) Snowbed L and F + H layers, and c) Birch Wood.

The observed ranges of soil moisture in summer, expressed as % of dry weight, were:

Lichen Heath (LH)	18- 100
Dry Meadow (DM)	80- 235
Wet Meadow (WM)	330-1215
Birch Forest (BF)	45- 290
Snowbed (SB)	18- 365

From the physical soil analysis we were able to calculate the mosture content at saturation. This occurs in early spring and late autumn in the top 4 cm:

$(Ao + A_2)$	LH	120
	DM	490
	WM	570
	BF	360
$(Ao + A_2/B)$	SB	200-250

The three Stigstuv sites (LH, DM, WM), when combined (Fig. 7a), provide a moisture gradient from the Lichen Heath (dry) to the Dry Meadow (dry to mesic) to the Wet Meadow (wet to very wet).

The surfaces in Fig. 7 are regressions of interactive temperature and moisture responses derived from 154, 58 and 55 data points for Stigstuv, the Birch Wood and Snowbed respectively. Each data point was a mean of three replicates. The equations are as follows:

Stigstuv (three sites together):

$$\text{Resp. } (\mu g\ C/g\ OM) = 0.426 + 0.035\ e^{0.165t} \times m - 0.00005\ e^{0.165t} \times m^2 + 0.00000002\ e^{0.165t} \times m^3$$

Birch Wood:

$$\text{Resp.} = 6.935 + 0.441\ e^{0.064t} \times m - 0.002\ e^{0.064t} \times m^2 + 0.000004\ e^{0.064t} \times m^3$$

Snowbed:

$$\text{L layer Resp.} = -0.434 + 0.028e^{0.16t} \times m - 0.0002e^{0.16t} \times m^2 + 0.00000065e^{0.16t} \times m^3$$

$$\text{F + H layer Resp.} = +0.483 + 0.076e^{0.109t} \times m - 0.00077e^{0.109t} \times m^2 + 0.00002e^{0.109t} \times m^3$$

The response of respiration to moisture (Fig. 7a) shows an optimum soil moisture content of 400-500%. Moisture contents below 300% as well as above 500% are correlated with a decrease in repiration rate. At the wet meadow there seems to be a positive effect of moisture again when it reaches "super moist" conditions at 1100-1200%.

At the Birch Forest site (Fig. 7c) respiration rate appears to rise up to a moisture level of approximately 150%. Higher moisture contents seem to decrease respiration, but not significantly within the moisture levels measured.

At the Snowbed site (Fig. 7b) the surfaces and regressions for the layers are given separately. Respiration increases in the L layer with increasing moisture while F + H layers react more like the Birch Forest. Optimal moisture content in the layers was not found within the observed range. In relation to moisture content at saturation it seems from these field measurements of soil and litter respiration that the optimal soil moisture content is close to 60-80% of saturation at the sites rich in organic matter, i.e. between 200-500%.

DM 60-80% of sat. = 295-390%
WM 60-80% of sat. = 340-455%
BF 60-80% of sat. = 220-290%

Calculated carbon loss in respiration experiments and its relationship with in situ weight loss

Carbon lost in respiration during the field season was calculated by multiplying the amount of C lost per gram dry weight organic matter for a discrete temperature/moisture period by the number of days in the period and by summing the periods over the season. The total loss was estimated at 0.0682 g C/g organic matter at the Wet Meadow compared with 0.0401 g C/g measured from litter bags over the summer.

These values are not very supportive of the view that "carbon dioxide evolved is closely related to the loss of organic material" (Witkamp, 1971). However, at the Dry Meadow site the predicted C loss was 0.053 g/g and the measured C loss was 0.050 g/g based on a carbon content of 50% and an average loss over the summer of 10% weight in litter bags (Heal & French, this volume). Other comparisons were as follows:

	Predicted C loss	*Measured C loss*
Snowbed	0.0095 g/g	0.013 g/g
Lichen Heath	0.018 g/g	0.018 g/g
Birch Wood	0.074 g/g	0.024 g/g

The field moisture and temperature levels and respiration rates in these experiments on two sites are presented in Fig. 8 and 9. The indications from Norwegian data are that in some circumstances respirometric determination of C loss does emulate observed C and weight loss. Certain other aspects of decomposition processes place constraints on the use of respirometry data for evaluation of decomposition rates. These will be discussed later in this paper.

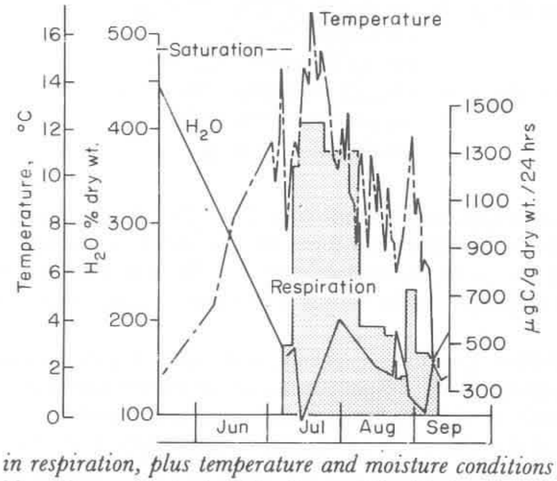

Fig. 8. Carbon loss in respiration, plus temperature and moisture conditions for the Dry Meadow site at Hardangervidda. Measurement of respiration was for 64 days between early July and early September. Optimal moisture was 60-80% of saturation, i.e. 295-390% (dry weight).

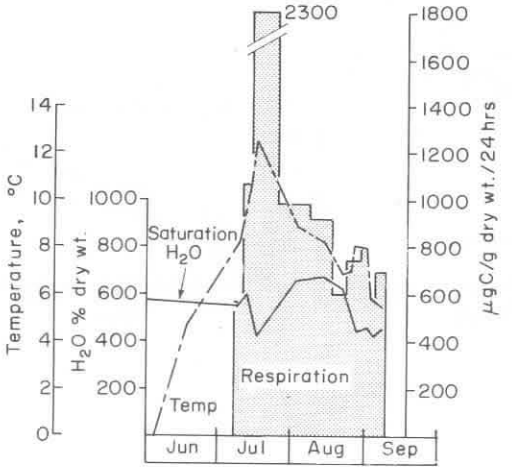

Fig. 9. Carbon loss in respiration, plus temperature and moisture conditions for the Wet Meadow site at Hardangervidda. Measurement of respiration was made over a 64-day period from early July to early September. Optimal moisture was at 60-80% of saturation, i.e. 340-455% (dry weight).

Moor House, Great Britain

From the British experiments a respiration response surface dependent on moisture and temperatures could not be constructed nor was it possible to ascertain how decomposer microorganisms would respire at extremes of temperature and moisture. The response of respiration at 10°C in *Rubus* to field moisture is given in Fig. 10a. To derive information on the influence of moisture, the regression of respiration on age has been used to "correct" *Rubus* respiration rates to time zero. The corrected respiration values (Fig. 10a) show a positive correlation with increasing moisture up to 200%. Above that, interpretation is tenuous but there is no indication of a decline in respiration at high moisture levels as observed at Barrow and Hardangervidda. Respiratory response to temperature variation at fixed moisture is shown in Fig. 11. Measurable respiration continues to −5°C and in the range between 0° and 20°C the response to temperature is best expressed by a $Q_{10} = 3.5$.

From data available and using Q_{10} values of 4 and 2 over the range of temperatures normally encountered in the Moor House site, it was possible to evaluate the extent to which litter bag weight losses at this site can be predicted from respirometry measurement of O_2 uptake during decomposition (Fig. 10c and d). Generally use of the $Q_{10} = 4$ temperature relationship gave results which correlated best with observed weight losses from litter bags. It is possible to approximate rates of decay in this case by extrapolation from a relatively small set of respiration data, provided a realistic value is given to the exponential temperature relationships. The accuracy of some of the predictions (Fig. 10c) is remarkable and may be reflecting that decay rates in Moor House litters are very steady and possibly primarily determined by substrate quality.

The regressions from litter bag and respiration data of four species over 3-4 years of sampling are given in Fig. 10b. *Rubus* and *E. vaginatum* show significant declines in respiration with weight loss while *Calluna* shoots and stems do not. Results for the *Calluna* residues most likely reflect a low proportion of readily decomposable substrates. In *Rubus* and *E. vaginatum* leaf materials, after an initial rapid weight loss has

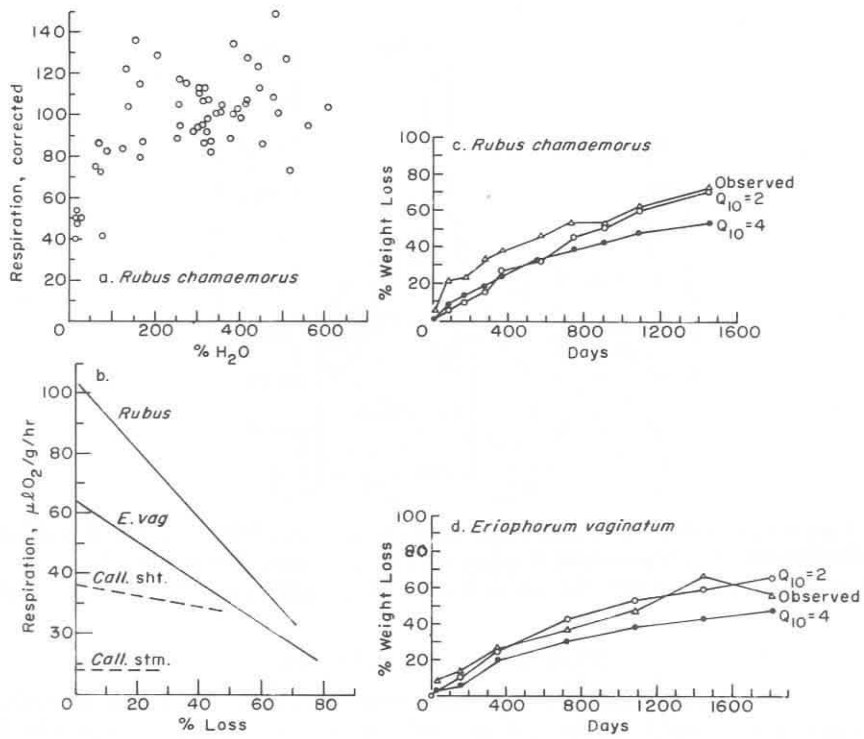

Fig. 10. Respiration (at 10°C) and weight loss of litters at Moor House, UK. a) Relationship of Rubus *litter respiration with moisture after age effects were "removed." b) Regression of respiration in litter bags with increasing substrate age. c and d) predicted and observed weight loss in* Rubus chamaemorus *and* Eriophorum vaginatum *respectively using the exponential* Q_{10} *= 4 or 2 to calculate.*

occurred and they more closely approach the chemical state of woody stems, the decline in respiration with weight loss is not statistically significant. Initial rapid weight losses in leaf litters may be due to leaching effects while in the case of later decay rates most of the loss is due to CO_2 respired through microorganism tissues whose biomass and maintenance requirements vary little between years.

Other Sites

Respiration data from an Alaskan birch forest site, a peat bog in Glenamoy, Ireland, and Signy Island, Antarctica, were donated by Dr. Keith Van Cleve, Dr. Paul Dowding and Dr. John Baker, respectively. Data from Alaska and Glenamoy are given in Fig. 12-14. From the Alaskan data temperatures increasing from 0-10°C increase respiration 3 to 4 fold (Fig. 12). Temperatures exceeding 35°C depress respiration in the birch litter, fermentation and humus layers. The quality effect of the decaying material on respiration rates is clearly illustrated in the slope of the response in the different layers at identical temperature ranges.

The moisture relationships of the layers in birch residues (Fig. 13) are not unlike those described earlier for the tundra litter and soils. Moisture levels above 300% depress respiration rates. Preliminary analysis of the data available does not show a shift in the mode for optimum moisture level when temperatures are changed. Optimum moisture is approximately 300% at any temperature.

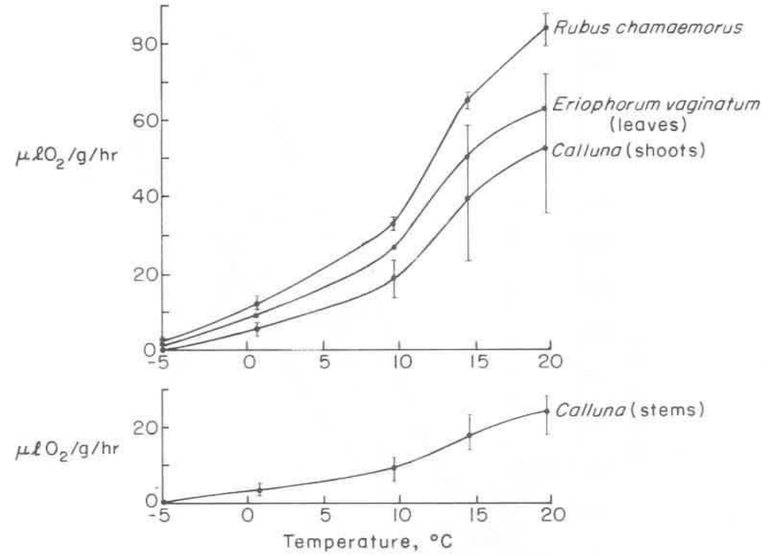

Fig. 11. Respiration in Moor House litters in relation to temperature. The mean, maximum and minimum of four samples are plotted. E. vaginatum *data based on single readings. Samples had been in the field for 6-7 years.*

The Glenamoy data (Fig. 14) show respiration responses for two plant species. Moisture increases the rate of respiration up to the 100-200% level, above which it remains constant or declines rather sharply, depending on the substrate.

The response curve differs slightly at different temperatures and there is an indication that temperature changes shift the moisture optima in both species. These data show again the vigorous interaction of moisture, temperature and substrate quality. The response of Glenamoy decomposer microorganisms to temperature changes has a Q_{10} of more than 3 but less than 4 (Dowding, pers. comm.).

Between Site Comparisons

It can be seen that in the Stigstuv drier sites low moisture is limiting the respiration rates while on the wet site, high moisture is limiting (Fig. 7a). The same relationship to moisture levels is seen throughout the moisture ranges examined at Site 2 at Barrow (Fig. 2b and 4). In both sites at 0°C a moisture content in the range 350-450% decreases respiration. However, the phenomenon was seen in Norwegian data after they had been recalculated to 0°C. Organic remains from both sites show an increase in respiration at the 800% level (Fig. 13). The increase can be up to 50% of the rate functioning at optimal moisture levels for a given temperature. In Barrow this phenomenon may be due to proliferation of such water moulds as *Pythium* and *Achlya* (Flanagan & Scarborough, this volume).

Respiration and decomposition in organic remains at Stigstuv and Barrow respond in approximately the same manner to variation in moisture. While data are not complete, preliminary analysis shows that in Hardangervidda sites at lower temperature the high moisture levels do not decrease respiration so sharply, so that here as in Barrow at low temperatures relatively high respiration continues, throughout a much wider range of increasing moisture levels. These conditions dominate in spring and fall.

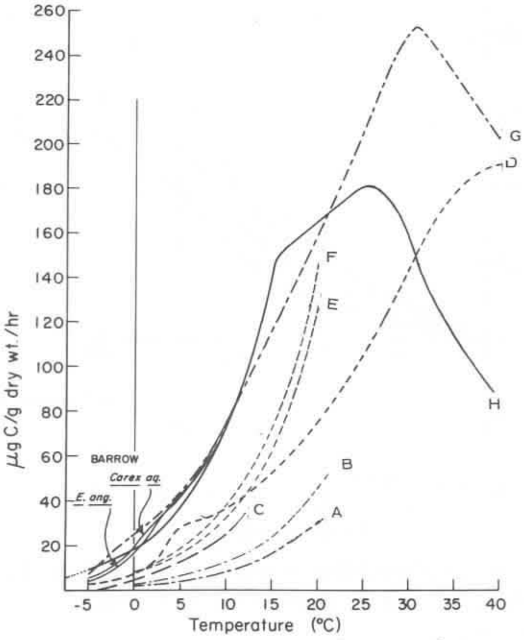

*Fig. 12. Respiration response to temperature of substrates in different national sites. A-Litter in Norwegian snowbed; B-Litter at Stigstuv combined (WM + DM + LH); C-*Dryas octapetala *litter at Eagle Summit, Alaska, US; D-Humus in Alaskan Birch forest; E-Alaskan birch F layer; F-Birch litter, Maurseth, Norway; G-Alaskan Birch litter; H-Barrow (Site 2) litter which is practically identical to one-year-old dead of* C. aquatilis *and* E. angustifolium. *All measurements were made at 100%* H_2O *(dry weight). Curves are eye-plotted.*

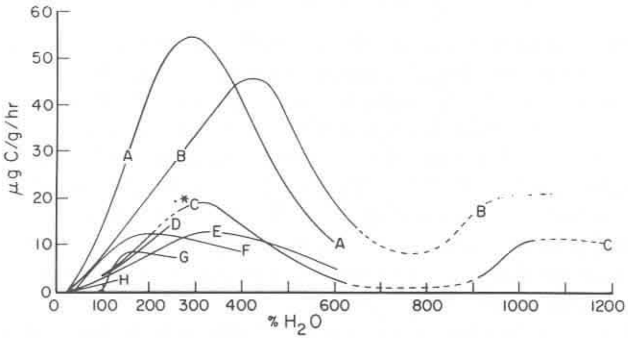

*Fig. 13. Respiration response of varying substrates to different moisture levels at 0°C. Dashed lines indicate that data were sparse, i.e. less than three samples and/or less than six readings per sample. A-Fairbanks Birch litter; B-Barrow litter; C-Wet meadow; *C-Dry meadow data correspond to this part of Wet meadow data. No data beyond 200%* H_2O *level. D-Snowbed (L); E-Fairbanks Birch (H); F-Birch (L+H); G-Snowbed (H); H-Lichen heath (H). Curves are eye-plotted.*

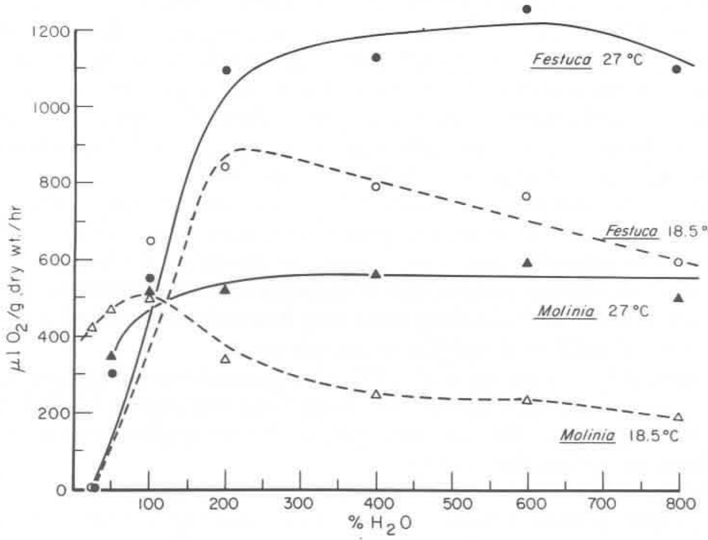

Fig. 14. Respiration in recently dead leaves of Molinia *and* Festuca *at 18.5° and 27°C with varying moisture at Glenamoy, Ireland. Points are the means of 4 samples, 6 readings per sample. Curves are eye-plotted.*

It can be concluded that at Barrow and Hardangervidda sites in the upper soil and litter little or no respiration goes on at moisture levels below 20% and that moisture from 20% up to 350% increases respiration while levels in excess of 450% depress respiration rates. Moisture and temperature are very interactive in both sites throughout wide ranges in both parameters. This interaction is minimised at low temperatures. Increasing temperature in Barrow Site 2 materials increases the respiration rate but decreases the optimum moisture level. This shifting of the optimum moisture with temperature is accentuated in the soil (Douglas & Tedrow, 1959). There are undefined qualitative and quantitative relationships between organic matter content of the substrate and the moisture optimum for decomposition. Both of these parameters exert their influence under the direction of temperature. Optimum moisture levels depend upon bulk density, percent organic matter and mechanical structure which in themselves are interrelated at all sites.

At Barrow Site 4 respiration in litter responds differently from that on Site 2 in that the negative effect of increasing moisture occurs at approximately 300% for all temperatures. The effect is most pronounced at the higher temperatures. Shifts in the optimum moisture for respiration when temperatures vary are not as evident in litters on Barrow Site 4 as they are in Site 2 litters.

At Glenamoy, Ireland, and the Alaskan taiga birch site moisture becomes limiting in the 100-200% and 200-300% ranges respectively. The Irish data reflect quality and perhaps microorganism population effects in the two different decomposition rates shown by the species studied.

The Moor House and Signy data show no decrease in respiration at the moisture levels influential at other national sites. There is some indication that at Moor House optimal moisture for decomposition is in the range between 200 and 600% (Fig. 10a). At Signy Island optimal moisture may be in the 600-900% range.

At the Barrow site *in vitro* oxygen enrichment studies were performed on the litter and it was shown that increasing moisture content of substrate had no influence on respiration rates. Oxygen enrichment eradicated the negative influences of increasing moisture but had no effect in retarding respiration at low moisture contents. Respiration and moisture measurements at Signy Island were performed on very loosely deposited mossy substrate. Here the possibility for adequate aeration of microorganisms even in very wet conditions exists and could explain why optimal respiration in this site continued at high moisture levels.

In three of the tundra areas studied (UK, USA and Norway) there was strong evidence supportive of the claim that respiration measurements in the laboratory or in the field allow us to predict actual weight losses in the field. At the same time caution must be exercised in making predictions. It appears that while reasonable predictions of weight losses in litter and standing dead may be made the method is not so dependable in the case of soils and soil/litter complexes.

We have taken 200% moisture and 20°C as representative of approximate optima for respiration in the Tundra Biome. By comparing respiration in different species and age of substrates the effect of these properties on respiration can be observed within and between substrates (Table 3).

The standard error about the mean figures is sometimes as high as 20% of the figure given. Nonetheless general trends within aging substrates and large differences between substrates emerge in comparing these data. The rates of respiration in Barrow and Moor House plant residues of one, two and more years old show the effect of substrate age on the release of carbon in respiration.

Respiration in Barrow litters on Site 4 is considerably lower than that in Site 2. No explanation can be offered other than to allude again to the possibility of differences in microorganisms, qualitative and/or quantitative, between the two sub-sites. The highest rate of carbon loss possible at these parameter values for the Stigstuv site is low compared with losses in most tundra sites. But in the Stigstuv sites we are referring to the upper 2 cm of soil with aged litter which reflects the decrease in respiration rates that occurs when organic matter enters the soil profile, having lost a considerable portion of its "soft" carbon fractions. The Barrow soil respiration rates (Douglas & Tedrow, 1959) compare most closely with Stigstuv data and emphasise that in the Norwegian site combined respiration in soil and litter was measured where the bulk density as well as quality has altered significantly.

Between-site variations in annual carbon losses in respiration are due to site differences in 1) length of decomposer season, 2) diurnal and seasonal climatic variables, 3)pH, 4) substrate quality and quantity, and 5) microorganism community structure as affected by availability of nutrients (N and P) and interaction with the microfauna community.

At many tundra sites a yearly weight loss of 10% in litter and leaf residues is not uncommon (Heal & French, this volume). Based on a litter mass of 250 g/m^2 one would require an average respiration rate of approximately 50 μl O_2/g hr for 100 days to account for a 10% weight loss, i.e. 25 g/m^2. The figure is within the range of respiration rates for Hardangervidda and Barrow litters even at low temperatures (less than 5°C) as long as moisture is between 200% and 500%. Therefore we are not obliged to seek other means such as comminution effect, leaching and/or length of decomposition season, i.e. of more than 100 days, to explain weight losses from litter in these sites.

At the Glenamoy site a respiration rate of 50 μl O_2/g hr is in the very low range, and because of the longer decomposition season and temperature ranges in the Irish and UK sites larger annual weight losses and respiration losses would be expected (much larger than 10%) than in sites with short (100 days) decomposition seasons and relatively low mean annual temperature.

Table 3. Comparison of carbon losses in respiration.

Site and substrate	*Temp (°C)*	*H_2O (%)*	*Carbon loss (µg C/g dry wt/hr)*	*Substrate age (yr)*
Barrow, USA				
Site 4, litter*	20.0	200.0	101.0	Heterogeneous
Site 2, litter	20.0	200.0	135.0	Heterogeneous
E. angustifolium leaves	20.0	200.0	145.0	1
	20.0	200.0	120.0	2
	20.0	200.0	95.0	3
C. aquatilis leaves	20.0	200.0	130.0	1
	20.0	200.0	110.0	2
	20.0	200.0	90.0	3
Hardangervidda, Norway Stigstuv				
Wet meadow soil/litter	20.0	200.0	80.0	Heterogeneous
Dry meadow soil/litter	20.0	200.0	80.0	Heterogeneous
Glenamoy, Ireland				
Festuca leaves	18.5	200.0	414.0	1
Molinia leaves	18.5	200.0	230.0	1
Alaska, USA				
Birch litter	20.0	200.0	240.0	1+
Moor House, UK†				
Calluna shoots	20.0	200.0	64.0	0.25
	20.0	200.0	80.0	1.0
	20.0	200.0	40.5	4.0
Calluna stems	20.0	174.0	33.0	2.0
	20.0	194.0	16.5	4.0
	20.0	188.0	16.5	5.0
E. vaginatum leaves	20.0	218.0	124.0	0.1
		215.0	80.0	.4
		228.0	143.0	1.0
R. chamaemorus leaves	20.0	208.0	200.0	.2
	20.0	176.0	53.0	2.0
	20.0	262.0	83.5	2.5

* Standard errors on Barrow data were never more than 7% of the figure given.

† Moor House figures extrapolated (from 10°C) using an exponential curve with $Q_{10} = 4$.

Despite variations in respiration and decomposition rates relative to site climatic differences there are significant differences within and between sites due to quality of litter input (Table 3).

The complexities inherent in making between-site comparisons could be decreased by eliminating time and quality influences and examining respiration rates between the sites for a fixed period of 100 days using a standard substrate which has undergone initial weight loss through leaching and decomposition of readily decomposable components. Plant residues in this state are composed chiefly of a lignocellulose fraction which should be of approximately the same quality in different sites. By this method the sites will be partitioned mainly by temperature, moisture and pH variables. To obtain these comparisons for respiration rates a new international programme would be required.

The foregoing statements are the expression of our present understanding of respiration in relation to temperature, moisture and weight losses which are constrained somewhat by those areas which are not covered in our resources of data from experiments and the open literature.

Comparisons with Other Areas

According to Witkamp (1966) oak forest floors in temperate zones evolve CO_2 at the rate of 400-500 ml/m^2 hr. Estimations for Barrow tundra, excluding estimated root respiration, are of the order 75-120 ml CO_2/m^2 hr (this is at average conditions of 5°C and 150% H_2O during the period June to August), i.e. at about ⅕ the rate for temperate forest floors. Havas & Maenpaa (1972) present data for a Finnish spruce forest soil (including plant materials but excluding mineral soil) showing CO_2 evolution from June-August at the rate of 153 ml CO_2/m^2 hr, which is only slightly higher than the rate measured and calculated for Barrow. Lundegardh (1927) and Monteith *et al.* (1964) made extensive studies on rates of CO_2 evolution from different soils under various conditions. Results in the two studies are in close agreement and CO_2 evolution ranged from 0.125-0.411 g/m^2 hr for agricultural soils to 1.0-2.0 g/m^2 hr for temperate forest floors. It was estimated that root respiration accounted for 30% of the CO_2 evolved. Root contribution to CO_2 released from Barrow soils may be much greater than in temperate area ecosystems. The below ground live root biomass in Barrow is five times that of above ground biomass (Tieszen, 1972) whereas in temperate woodlands the ratio may be reversed (Satchell, 1971). If root contribution to soil respiration at Barrow is as much as 50% then the range for CO_2 production from Barrow soils, minus root respiration, is 0.147 to 0.235 g CO_2/m^2 hr. Aristovskaya & Parinkina (1972) in USSR IBP studies examined tundra soils of the Taimyr Peninsula and found that maximal CO_2 evolution was 0.760 g/m^2/30 min and the minimal release was 0.011 g/m^2/30 min. The mean between these extremes is 0.77 g/m^2 hr. If root and algal respiration = 50% of CO_2 released, 0.38 g CO_2/m^2 hr is the average respiration rate for Taimyr tundra. This figure is close to the calculated range for the Barrow system. The respiration process in temperate areas continues throughout 365 days. Tundra at Barrow has a respiration season of at least 100 days. By decreasing the season in temperate areas to 100 days, thus increasing hourly rates of CO_2 release by 3.65 times, and decreasing the hourly rates by 30% in relation to root respiration, a comparison between tundra and temperate regions can be attempted. The calculation indicates that agricultural and temperate forest soils lose CO_2 through microorganism metabolism at 3-6 and 25-30 times, respectively, the rate for the Barrow system. In this result we have not accounted for differing amounts of organic matter per m^2 in the different systems. An adjustment of the figures relative to grams of organic matter in the systems would provide a much better basis for comparison.

The estimates presented are only calculated and theoretical. This caution, to a large extent, applies to many of the calculations presented in this paper because in several cases data are inadequate. Yet they do allow us to see that present results fall within expected ranges.

Havas & Maenpaa (1972) have shown soil respiration continuing down to −3°C beneath the snow in a spruce forest. Response to temperature in their site has a $Q_{10} = 3$. Van Cleve (pers. comm.) has measured respiration at sub-zero temperatures in Alaskan birch forests and unpublished data of the senior author on alpine tundra in Alaska show respiration continuing at −5°C in litter residues of *Dryas octopetala*. Decomposition at sub-zero temperatures in tundra regions possibly extends the microbial metabolism season by as much as two months beyond the plant production season.

Zimenko & Revinskaya (1972) showed that in peat-bog soils of the Minsk state farm, moisture levels in excess of 40% of the pore volume decreased decomposition rates. Ilyaletdinov & Suleimenova (1971) established that mineralization of organic matter in soils of the Kzyl-Orda region of Kazakh SSR was severely decreased by flooding. This effect was amplified if flooding occurred early in spring. Spring flooding occurs in most tundra sites. Yamane & Sato (1967) showed that in flooded soils increasing temperatures accentuated the negative effects of high moisture.

The effects of different moisture levels on microbial respiration in tundra organic remains and the interactions between temperature and moisture are not unusual or extraordinary phenomena. Similar relationships have been remarked upon previously for *in vitro* experiments with microorganisms by Ayerst (1968), Chen & Griffin (1966) and Waksman & Gerretsen (1931). Moisture and temperature interactions in soils litter and humus are reported by Kärenlampi (1971), Mikola (1960), Mork (1937-1939) and Witkamp (1966). The latter publications do not stress the negative influences of high moisture on respiration. It is likely that field conditions in their sites never reached such high moisture levels as those encountered on tundra at the time of thaw and in fall when rains fail to penetrate a rising permafrost pan.

At this point it may be constructive to reiterate how within- and between-site estimates and comparisons of carbon and weight losses are affected by certain constraints.

1. Respiration measurements are not an end in themselves. They are made for a variety of reasons. The measurements allow us to calculate carbon loss through the microbe compartment doing the decomposing.

This assumption holds true enough for litter and standing dead which can be removed, handled and placed in respirometry flasks with minimal disturbance of resident microbes. Using the method with soil and humus, we are still abysmally ignorant of what we are truly monitoring. In using direct respirometry on soil we are unable to distinguish between microfloral, microfaunal, root and algal respiration and there is a compounding flaw in Gilson respirometry experiments where soil is removed and placed in respirometry flasks because soil is completely altered in its structure, moisture content, surface area, etc. The interpretation of soil respirometry experiments is still a very difficult matter.

2. Moisture, temperature, substrate, and pH all interact in combination on decomposer microorganisms and while moisture and temperature may be the most influential agents involved it is informative in this connection to study the effects of moisture and temperature on individuals of the major species components of decomposer communities.

This work has begun on the organisms of the US sites at Barrow and Eagle Summit. Some preliminary data are included here to help shed some light on the responses in litter measured in respirometers. At the risk of repetition, it is the organisms doing the decomposing whose response we measured in respirometers. The major species present at any one time change due to a variety of causes, not least the competitive saprophytic abilities of organisms (Garrett, 1963). Different organisms have different responses to temperature, pH, and moisture so that the response surfaces of respiration processes will change according to the physiology of the dominant decomposers present. Fig. 2 and 4 in Flanagan & Scarborough (this volume) illustrate these points. Differences in organic matter respiration within and between sites are probably partly caused by just these sorts of differences between organisms.

3. The influences of moisture and temperature on respiration within and between tundra sites are modified by the quality and quantity of the decomposing organic matter. Both influences of organic matter are interwoven with the moisture and temperature influences. Generally, the higher the organic quality of any organic substrate the less negatively is respiration influenced by increasing temperatures above optimal levels. The height of the temperature/moisture response surfaces decreases with decreasing quality of organic remains. These trends are indicated in Fig. 5, 10b and 12. In soils these influences are magnified in proportion to depth (*vide* Douglas & Tedrow, 1959) and rate of accumulation of antibiotic agents and/or metabolic toxic products such as tannins, alkaloids and terpines. These latter are part of the quality effect.

4. The problems inherent in recalculation and extrapolation of field and laboratory data are, in most cases, self evident. However, when calculating carbon loss and comparing it to litter bag weight losses some problems arise. It is essential to consider here the differences between loss of carbon during maintenance respiration and respiration processes involving growth of the decomposer microorganisms. Fungi can assimilate 20-40% of carbon for growth while bacteria may incorporate as little as 5-10% of their carbon source. These are maximal assimilation figures (Waksman, 1932). This microorganism biomass remains in substrates in litter bags and is not shown as a weight loss; therefore the method underestimates dissolution rates of substrates. Estimates of carbon loss and decomposition rates from respirometric experiments also exclude microorganism incorporation of carbon so that both of these most common measures of decomposition rates taken on face value will give an underestimate of real rates for dissolution of organic residues. The respiration measure does allow for a reasonable correction to be made for growth of microorganisms and therefore a truer figure for substrate dissolution rates can be obtained. To emphasise this point consider the predicted weight loss in Fig. 6. Based on respiration data 11.8% weight loss could occur over the ranges of temperature and moisture occurring during the period. Based on litter with a carbon content of 54% the actual loss due to respiration would be 0.064 g/g, i.e. 54% of 0.118 g/g. If maximal decomposer growth was occurring at the same time then carbon was being extracted from substrate at the rate of 0.088-0.095 g/g. This would mean that a substrate composed of 54% carbon was losing carbon at about 0.09 g/g total and therefore the total weight loss, because of substrate dissolution, could be in the order of 0.187 g/g or 18.7%. This is almost double the field measurements for the period in question.

Clearly we must consider the organisms even more closely since these figures do not include a further loss of carbon as waste products other than CO_2. If the carbon assimilated in microorganisms remains within the litter as live or dead microbial tissue or waste products then the weight remaining in litter bags includes the carbon in growth, and direct comparisons of measured and predicted weight losses are valid.

The errors are most serious, however, when we interpret the data as rates and avenues of carbon cycling and assimilation.

5. The production of gases other than CO_2 in soil systems is well known. Lynch (1972), Lynch and Harper (1974), and Ilag and Curtis (1968) attest to the potential microorganism production of significant quantities of ethylene in soil. Clymo & Reddaway (1971) and Svensson (1973) showed that methane production may account for as much as 15% of the total carbon lost from tundra soil in gas form. Svensson (1974) discovered at Abisko (Sweden) that of total gaseous carbon losses methane constitutes less than 1% from dry, elevated tundra but up to 50% in waterlogged depressions. Dunican & Rosswall (this volume) comment on methane production in tundra at Devon Island (Canada), Hardangervidda (Norway) and Barrow (Alaska, USA).

Between- and within-site comparisons of decomposition rates and comparisons of carbon loss with weight loss in future studies, especially in soils, should address carbon losses in the form of gases other than CO_2, otherwise low estimates will be obtained of carbon cycling and decomposition rates. We have not considered it here other than to realise that carbon and weight losses may occur in tundra due to methane and ethylene producing processes.

CONCLUSION

We have learned much from our studies of respiration and decomposition in tundra plant residues. There are some very strong common trends shown in response to temperature and moisture at different tundra sites.

The literature cited corroborates the result of investigations on tundra respiration and decomposition as influenced by moisture and temperature. We are tempted to conclude therefore that the majority of tundra microorganisms respond to moisture and temperature like microorganisms anywhere, and that in large part the processes of decomposition are basically the same in tundra as elsewhere. For the amount of organic materials produced each year the resident microorganism and leaching processes can recycle as much organic matter, proportionally, as is recycled in temperate or boreal regions. Respiration and, most likely, decomposition can occur at very low temperatures (−7°C), reflecting the presence of some very cold-tolerant and or psychrophylic microorganisms in tundra. Tundra moisture levels depress decomposition at the low (20%) as well as at the high (400%-2000%) range. Tundra temperature/respiration relationships are best expressed by an exponential $Q_{10} = 4$ and are better correlated than are moisture and respiration.

Much more needs to be learned about soil respiration levels and response surfaces. The most striking need is for students of decomposition in tundra or elsewhere to return to the study of microorganisms responsible for processes and to learn the major group present in succession of decomposition. This knowledge will allow a much clearer understanding of respiration data. Many of the major decomposers of tundra organic matter within sites behave differently physiologically. These differences are probably accentuated in between-site comparisons. Therefore it is to be expected that significant differences and similarities in decomposition rates and responses will emerge in synthesis studies. The differences and similarities are those to be found amongst major microorganisms in the sites. Knowing how the major decomposer organisms respond will tell us how the decomposition processes respond. Studies should start with the major organisms and proceed to the process; only then can comparisons be made.

Modelling of microbiological successions and associated decomposition processes may begin at any time from the beginning to end of the study so long as the final simulation model incorporates the enrichment distilled from study of the microorganisms responsible for the processes.

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